Understanding the causes that underlie variation in diversification rates across a phylogeny requires a quantification of the pattern of that variation. Speciation rates may be recovered from phylogenies of living species, as there are observed speciation events recorded in those data. However, extinctions are not recorded in phylogenies of living species, and so the estimation of extinction rates in the absence of fossils has proven contentious (1–4). For groups with well-documented fossil records, extinction and speciation rates may be estimated using the patterns of repeated occurrences through time of individual species (5–7), however much of life’s diversity is partitioned in clades with poor fossil records. For groups with poor fossil records, combining a phylogeny of extant species with even a few extinct lineages has been shown to dramatically improve estimation of extinction rates (#Mitchell et al. bioRkiv).

Here, we analyze a phylogeny of 469 living species of Caudata from (8) with 75 extinct species added according to their topological position (9) and with the branch lengths stochastically pulled from the *cal3* distribution from (10). Placing the extinct caudates on the molecular tree involves uncertainty in both the topological position of the extinct species and in the branch lengths that connect them. We used seven different topologies for the extinct species, and performed ten different time-scaling procedures on each topology, to assess the impact of these sources of uncertainty on our inference of diversification patterns (see SOM for all trees). The only topology that produced a significant deviation was one where the extinct clades Scapherpetonidae and Batrachosauroididae were sister to one another and outside Urodela, and the deviation was restricted to a spike in rates at the origin of the extinct clade in the late Cretaceous. We estimated the rates for the *cal3* time-scaling using by fitting an homogenous birth-death process to the extant-only tree, which means that all fossil tips had branches pulled from the same rate distribution, potentially limiting our ability to detect heterogeneity. Each of the 70 trees (10 time-scaled replicates of the 7 topologies) were then analyzed using BAMM.

Fossils occur throughout the history of the clade, with the oldest caudates in the tree from the Middle Jurassic (*Urupia* and *Koktarus*; #CITE) and the oldest urodeles included here from the Late Jurassic (e.g., *Qinglongtriton*; #CITE). The most diverse group, the Plethodontidae, has only a single demonstrably distinct fossil species, and relatively few occurrences of living species (11). This paucity is probably attributable to the habitats occupied by these lineages, although the model implemented in BAMM currently does not allow for clade-specific preservation rates. We analyzed all of the trees with both ~70% of plethodontids in our tree, and plethodontids reduced to a single tip for a sampling fraction of ~0.2%. Given the lack of fossils within Plethodontidae, results from the extant-only and extant + extinct runs were nearly identical for that clade, so we focus on the non-plethodontids (i.e., the portion of the tree with fossils) here, and present analyses of the full trees in the SOM.

Including fossil data in the phylogeny has relatively little impact on the estimation of speciation rates; although the values for particular lineages are slightly higher when fossils are included, the relative magnitude of speciation rates among clades are comparable. This is expected, as speciation rates are reliably estimated from extant-only data as the phylogeny preserves some speciation events (i.e., the potential range on speciation events has a lower bound at N-2). Extinction rates, on the other hand, are radically different when fossils are included (Fig 2). Not only are the rates higher both through time (Fig 2A), but the pattern of which clades have high extinction relative to others varies substantially (Fig 2B).

Given that speciation and extinction rates are both higher when fossils are included, the pattern of turnover and the expected lineage duration varies substantially. The combined analysis supports overall turnover rates within Caudata nearly twice what the extant-only analysis recovers (turnover, speciation + extinction, of 0.10 in the combined analysis versus 0.06 in the extant-only analysis).

Materials and Methods:

*BAMM Analyses*:

Each BAMM analysis was run for 100,000,000 generations, and shift configurations were sampled every 100,000 generations. The first 10% of each analysis was discarded as burn-in, leaving 900 sampled shift configurations per tree for analysis. Priors on the speciation and extinction rates were set using setBAMMpriors from BAMMtools (12), and the expected number of shifts was set to 200 per (13). Effective sample size was computed as a test for convergence using the R package coda (14). All analyses had effective sample sizes of at least 200 for both the log-likelihood and the number of shifts, indicating convergence.

All trees were analyzed both with the 70% of plethodontids included and in a reduced form with only a single plethodontid lineage (sampling fraction of 0.02%). The number of fossil occurrences across the whole tree was 160, although 22 of these occurrences are assignable to living lineages of plethodontid and one is an extinct species of plethodontid. Fossil occurrences were defined using the criteria outlined in (#Mitchell et al., bioRkiv) and represent stratigraphically unique occurrences of identifiable lineages (e.g., *Jeholerpeton* has only a single occurrence in our analyses, despite thousands of specimens, due to the fact that all specimens are known from a single formation, and detailed locality information is unknown).

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SOM:

Fossil group topologies guide

1:10 – Scap sister to all, Batrach sister to Crypts (S,((B,Crypt),Others)))

11:20- Scap sister to Crypts, Batrach sister to all (B,((S,Crypt),Others)))

21:30—Scap outgroup to crown, Batrach outgroup to Scap+Crown (B,(S,Crown))

31:40—Scap and Batrach sister to each other, outgroup to crown ((B,S),(Crown))

41:50—Scap sister to Batrach + Crown (S,(B,Crown))

51-60—Scap sister to crown, Batrach sister to Hyno+Crypt (S,((B,(Hyn,Crypt)),Others)

61-70—Batrach sister to crown, Scap sister to Hyno+Crypt (B,((S,(Hyn,Crypt)),Others)